ON THE ANATOMY OF THE BRITISH SPECIES OF THE GENUS *PSAMMOBIA*.

By H. H. Bloomer, F.L.S.

Read 11*th November*, 1910.

PLATES IX AND X.

Psammobia vespertina (Chemnitz).

The animal, in a quiescent state, lies with the valves of the shell a little agape, the adductor muscles partly relaxed, and the pallial lobes, excepting near the beak and ligament, protruding some distance beyond the edge of the shell, especially those portions bordering the pedal aperture (Fig. 1). Externally nearly the whole of the projecting parts is covered with the usual dusky-brown periostracum, which passes from the shell to near the mantle-fringe. In a normal condition the free edge of the lobes curves inwardly, so that the fringe is not often exposed to view. The exposure, however, may take place immediately preceding and during the process of moving, when the animal approaches complete expansion, and the pallial margin is uncurved.

The foot (Fig. 2, *F.*) is of a milk-white colour, very muscular, yet very sensitive. It can be protruded a great distance, and shows considerable power of mobility, projecting from any part of and moving all along the pedal aperture, bending from side to side, swelling or contracting, lengthening or shortening, and capable, either rapidly or slowly, of continually changing its shape and position. From my own observation the mode of locomotion is either by leaping or creeping, and in this function the foot plays the principal part. In leaping the foot is pushed out anteriorly with a slow, undulatory movement; whilst lengthening, the distal end bends, and passes underneath the other portion, then, with great rapidity and muscular force, it is straightened, and the animal thrown forwards. On the other hand, the foot may be thrust out sideways, passed underneath the shell, and with the same action the animal is turned over or sent some distance laterally.

In creeping, the distal end of the extended foot seizes the ground, contracts, and draws the body along, It is possible that this species also swims in the same manner as the smaller ones, but I have never seen it do so.

External Characters. — An average-sized animal measures about 52 mm. antero-posteriorly by 28 mm. dorso-ventrally. Dorsally it is curved with a depression under the hinge region. The other sides are likewise curved, except the postero-ventral part, which is angular, and projects more posteriorly than any other portion.

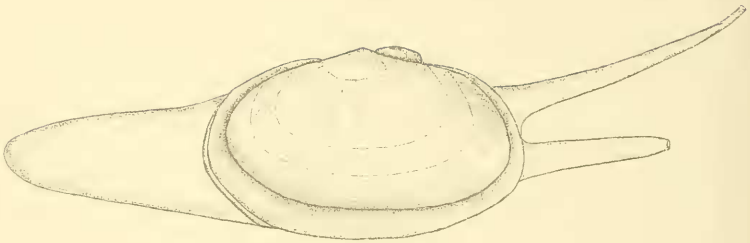
The pallium, or mantle, is a thin membraneous covering bordered by a muscular band, decreasing in depth as it passes rearwardly. The pedal aperture reaches from the anterior adductor muscle to the musculus cruciformis, consequently, between these two points

the apposed mantle-edges nowhere coalesce, but near the latter muscle the inner longitudinal fold, or velum, of the one mantle-lobe becomes fused with that of the other lobe. The united part then diverges from its relative position to the pallial edge, and, proceeding dorsally, separates only to become connected on each side with the lateral walls of the siphon. The apposed folds again become fused, and afterwards pass around the posterior and dorsal parts of the posterior adductor muscle. Thus the posterior portion of the pallial cavity is completely enclosed with the exception of the siphonal apertures. The inner longitudinal folds are also fused over the anterior (Fig. 5) as well as the posterior adductor muscle, and consequently form the covering of these muscles. Fig. 6 presents typical mucus glands of this portion of the pallium, and their ducts will be seen passing between the epithelial cells to the outer surface. Mucus glands, cells, or masses are present all round the inner surface of the mantle-lobes just above or below the velum. The pallium is apparently perforated by both the large adductor muscles, and its line of attachment passes on each side from the anterior adductor to the body of the animal, ascending as it goes rearwardly until over the branchia, where it is near the dorsal surface, then, descending, it skirts the edge of the posterior adductor muscle. Each mantle-lobe carries a tentacular fringe at the distal edge of the middle longitudinal fold.

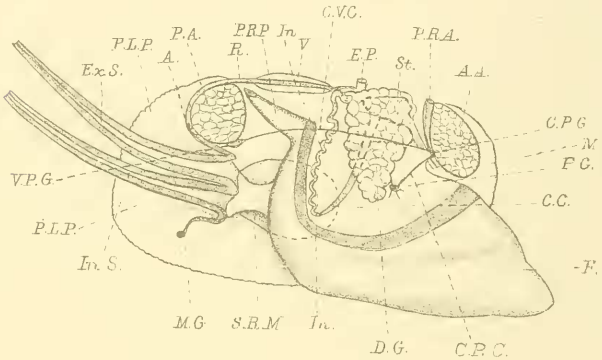
Underneath the posterior adductor muscle is situated the siphon. It consists of two long tubes (Fig. 2, *Ex.S.* and *In.S.*) capable of great elongation and contraction. The lower or inhalent is longer than the upper or exhalent one, and, in an extended condition, both, at the free end, usually curve upwards. The lower portion of the proximal part of the exhalent tube is united with the upper portion of the inhalent one, and the combined part (Fig. 2, *S.R.M.*) projects some distance into the pallial cavity. On each side of the animal the siphonal muscles are continued as a short thick muscle which penetrates the thin membranous pallial wall, and spreads out into a large flat ovate-shaped disc, with its external surface attached to the shell. Each tube generally carries at its extreme free edge six papillæ, whilst along the external surface is a corresponding number of rows of them, each row being in alignment with one of the papillæ at the free end. The position of each row is radially in a line with one of the internally arched muscle-masses mentioned farther on. It is further to be observed that the pallial lobes extend some distance posteriorly beyond the proximal portion of the siphon, and the siphonal tubes can be quite withdrawn between them (Fig. 2, *P.L.P.*). In this state the posterior portion of the branchia is forced into a folded position.

Pallial Muscles.—The muscles of the pallial edge form a band, diminishing in depth as it proceeds posteriorly. They consist principally of transverse muscle-fibres, radiating as from the umbonal region to the edge of the pallium, and longitudinal ones running chiefly near and parallel to the circumpallial edge.

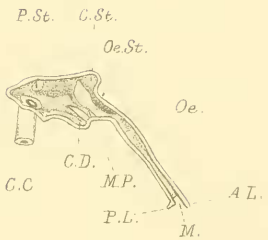
The siphonal tubes proximally become somewhat flattened. Their muscular wall is composed of five coats, alternately circular and



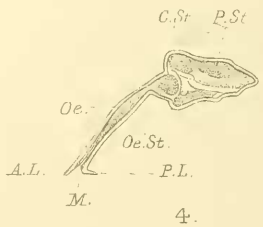
1.



2.



3.



4.

6.

5.

Sowerby del. ad nat. Huth lith. London.

ANATOMY OF THE BRITISH SPECIES OF PSAMMOBIA.

longitudinal in direction, beginning from the outside. The outer longitudinal muscles form a broad band, whilst the inner longitudinal ones are grouped into six semicircular masses facing inwards. Running from the outer to the inner annular band are a number of muscle-fibres constituting the transverse muscles which pass between the longitudinal muscles and through the middle annular band. At the proximal end of each lateral side the muscles of the siphonal tubes are drawn together into a short rounded muscle, which quickly spreads out into a large disc and forms the enlarged portion of the siphonal retractor muscle that is inserted into the shell. As before mentioned, the siphonal tubes are capable of not only great elongation but also of great contraction. In the latter case the contracted tubes often widen to large dimensions, whilst the proximal portions are partly introverted into the pedal cavity.

The anterior adductor muscle (Fig. 2, *A.A.*) is wide, convex on the dorso-anterior surface, slightly concave on the ventro-posterior surface, and spreads out towards the ends, which conform to the curvature of the shell. On the convex surface it is attached to the pallium, and on the dorso-posterior surface to the anterior retractor and anterior protractor muscles.

The posterior adductor (Fig. 2, *P.A.*) is a large muscle spreading out towards the ends, and likewise conforming to the convexity of the shell. It is attached to the pallium, except at the antero-dorsal surface, where the bifurcations of the retractor pedis posterior muscle rest upon it.

The musculus cruciformis (Fig. 2, *M.C.*) situated at the postero-ventral edge of the pallium, and ventrally to the posterior adductor muscle, is divided at each end into two branches. One branch proceeds some distance anteriorly and buries itself in the mantle-lobe, then, emerging on the outside, is inserted into the shell. The other branch goes some distance dorso-posteriorly, and in a like manner also becomes attached to the shell.

Pedal Muscles.—The foot (Fig. 2, *F.*) is large, very muscular, and capable of great expansion. The intrinsic muscles are annular, longitudinal, and transverse. The annular muscles constitute the pedal integument, and near its lateral inside walls run the powerful longitudinal muscles which traverse nearly the whole length of the foot, whilst passing from side to side are transverse muscle bundles; in the proximal part they are of some length and pass through the viscera, the ends spreading out and going between the longitudinal muscles to the integument; in the middle of the foot they also occupy the central area, having spaces between them which form the pedal sinus, but towards the distal end they, together with the longitudinal ones, fray out, resulting in a large muscular meshwork.

The retractor pedis anterior muscles (Fig. 2, *P.R.A.*) are short and thick, but not bifurcated; they pass dorsally along the rear side of the anterior adductor muscle, and are inserted into the shell close to the latter, and the fibres of their proximal part pass ventrally through the foot, spreading out fan-shaped.

The protractor pedis anterior muscles are large but short, and

adhere laterally to the sides of the shell, whilst anteriorly they are connected with the anterior adductor muscle. Proximally their fibres pass over those of the retractor pedis anterior muscles, and terminate in the pedal integument.

The retractor pedis posterior muscle (Fig. 2, *P.R.P.*) is also thick and short, with its two short bifurcations lying on the antero-dorsal surface of the posterior adductor muscle, and its distal ends attached to the shell, in close proximity to the adductor muscle. The fibres of its proximal part are traceable running in a longitudinal direction just inside the pedal integument.

The elevator pedis muscles are situated anteriorly to the centre of the dorsal edge of the foot, and their muscle-fibres are likewise soon buried in the pedal integument.

Alimentary Canal.—The mouth (Figs. 3 and 4, *A.A.*) is situated on the ventral surface close to the anterior adductor muscle, and is bordered by the lips which are continued laterally as the labial palps (Figs. 3 and 4, *A.L.* and *P.L.*). The œsophagus (Figs. 3 and 4, *Oe.*) is long and dilated from the centre to near the stomach. Its length and direction (the latter being more or less dorso-posteriorly) depend upon the expansion or contraction of the foot. The stomach (Figs. 2, 3, and 4, *St.*) is an irregularly shaped and several-lobed sac occupying the dorsal part of the visceral mass, and surrounded by the digestive gland or liver (Fig. 2, *D.G.*). It may be conveniently separated into the following divisions, œsophageal, cardiac, central, and pyloric, each being distinguished from the others by an internal raising or folding of the gastric wall, or the varying length of the cells of the epithelial lining. The œsophageal division (Figs. 3 and 4, *Oe.St.*) is small; it opens into the œsophagus at the fore-end, and posteriorly is bordered by the folded gastric wall, which here culminates in a very prominent process, separating it from the cardiac division. The cardiac division (Figs. 3 and 4, *C.St.*) is small, and continues on the left side as a deep pocket-shaped cavity. On the right side its separation from the pyloric division is indistinct. The above-mentioned process is a large and wide projection from the left side of the stomach between the various divisions, and is supported by a dense mass of fibrous connective tissue. The cells of the epithelium lining this and the adjacent parts of the stomach are extremely long and narrow. Under this process is the central division (Fig. 3, *C.D.*), a small round cavity receiving the large duct from the digestive gland. The pyloric division (Figs. 3 and 4, *P.St.*) is large, and embraces the greater portion of the stomach. On its ventral surface, towards the rear end, it is continued as a very long, slightly posteriorly, curved sac, the cæcum of the crystalline style (Fig. 3, *C.C.*). The crystalline style extends all along the cæcum, bends anteriorly on entering the stomach, and stretches along it to the anterior wall, frequently at this point it curves, and nearly fills the cardiac division as well.

Covering the floor of the stomach and entering the different cavities is a gelatinous mass, the flèche tricuspide, which, when stained with Ehrlich's hæmatoxylin, appears to be quite structureless, whilst the neighbouring crystalline style exhibits certain concentric markings,

and in the centre the matrix has, under high magnification, a mottled appearance.

Fig. 7 is a transverse section of the cæcum of the crystalline style and intestine, and shows the epithelium of the former to contain long columnar cells with the nuclei near the centre, and the free ends carrying a mass of long cilia. The cells increase in length as they approach the passage leading to the intestine. This passage apparently can be closed by a prolongation of the divisional wall which projects into the lumen of the intestine. In the same figure can be seen the typhlosole in the ascending intestine.

As the cæcum of the crystalline style and the fore-part of the intestine are in one piece, the latter has the appearance of being a somewhat constricted groove on the left side, and the intestinal wall only becomes complete at the distal end of the cæcum. The intestine turns dorsally, its wall is invaginated, forming the typhlosole, and near the posterior part of the stomach makes a number of folds; afterwards, turning posteriorly, it proceeds as the rectum, and is shortly encircled by the ventricle. It then passes over and partly round the posterior adductor muscle, enters the pallial chamber, and terminates with a small anus.

The digestive gland surrounds the stomach, but the greater portion lies ventrally to it. The large duct enters the central division from the right and larger lobe, and the other duct from the left and smaller lobe enters the anterior end of the pyloric division on the left side.

The renal organs, which are of an orange-red colour, are situated on the outside and over the pedis retractor posterior muscle, and adjoining the pericardium.

The animals examined are unisexual, the organ being situated around the digestive gland.

Regarding the branchia Dr. Ridewood[1] states that the inner demibranch hangs much lower than the outer, and the ascending lamella of the latter rises considerably above the level of the gill-axis, forming a supra-axial extension. The gill lamellæ have enlarged principal filaments with a grooved frontal border.

The number of filaments in a plica varies from twenty-four to thirty, and are the same in both demibranchs. There is a fairly large blood-tube in the sub-filamentar tissue in the apex of the plica, and all the interlamellar septa, and not the alternate ones only, extend high up the demibranch. The ordinary filaments present no exceptional features. There is a fair amount of muscle-fibre around the interlamellar spaces and in the interlamellar septa.

Nervous System.—The cerebro-pleural ganglia (Fig. 2, *C.P.G.*) are far apart, and situated between the adductor and the anterior retractor muscles, and close to the ventral surface. They are joined by a commissure passing close to the adductor muscle and in front of the œsophagus. Each ganglion sends out anteriorly a nerve which

[1] "On the Structure of the Gills of Lamellibranchia": Phil. Trans., B. cxcv, p. 248, 1903.

innervates the anterior adductor muscle and the fore-part of the mantle-lobe, and continues as the circumpallial nerve, which apparently joins the posterior pallial nerve. The viscero-parietal ganglia (Fig. 2, *V.C.P.*) are situated near the antero-ventral edge of the posterior adductor muscle. Each cerebro-visceral connective (Fig. 2, *C.V.C.*) passes outside the pedis retractor anterior muscle alongside the viscera, and between the transverse pedal muscle until near the retractor posterior muscle, when it pierces the pedal integument and then proceeds outside the retractor muscle to the viscero-parietal ganglion. Ventrally from each cerebro-pleural ganglion passes the pedal connective (Fig. 2, *C.P.C.*), which goes along the longitudinal and between the transverse muscles of the foot until it reaches the pedal ganglion (Fig. 2, *P.G.*) situated just in front of the digestive gland, but nearly buried in a transverse muscle-bundle. The branchial nerves leave the viscero-parietal ganglia on the posterior side, and, curving, run along the base of the gills. Posteriorly from the viscero-parietal ganglia run the posterior pallial nerves, which innervate the posterior adductor muscle, the siphon, and the posterior portion of the mantle-lobes. The nerve which innervates each siphonal tube is divided into six branches, each branch running along it to the distal end.

The sense organs, as well as the distribution of the finer nerve branches in the siphon and the mantle-lobes, are fully described by Rawitz in his work *Der Mantelrand der Acephalen*.

Psammobia Ferroensis (Chemnitz).

External Characters.—The one animal examined measures 21 by 10 mm. The dorsal surface is somewhat triangular, with a depression on the posterior side. The anterior part is curved, whilst the posterior is quite angular. As in *P. vespertina* the ventral portion of the latter projects backwards. The ventral side is only very slightly curved. Further, the animal is not so deep as *P. vespertina*.

The concrescence of the mantle-lobes appears to be the same as in *P. vespertina*, but the proximal portion of the siphon extends a little more anteriorly. The siphonal tubes are long, and in Fig. 8 it will be observed how the central part widens when wholly or partly withdrawn (*Ex.S.*). The anterior adductor muscle (Fig. 8, *A.A.*) is wider than it is deep, and shows a constriction at the centre of the under-surface. Compared with *P. vespertina* it is comparatively a smaller muscle, being shorter and shallower, and at the same time situated in a more oblique position. The posterior adductor muscle (Fig. 8, *P.A.*) is slightly angular at the dorso-anterior edge, and differs from that of *P. vespertina* in being relatively not so deep, but shorter and wider.

Alimentary Canal.—The œsophagus (Figs. 8, 9, and 10, *Oe.*) is moderately long, narrow, and curved. The stomach is divided into several lobes, as in *P. vespertina*, but the œsophageal division (Figs. 9 and 10, *Oe.St.*) is small and triangular in shape. The demarcation of the cardiac division (Fig. 10, *C.St.*) is well defined on the right side, but not on the left. The pyloric division (Figs. 9 and 10, *P.St.*)

is large and opens on the ventral side into the cæcum of the crystalline style (Fig. 9, *C.C.*), the latter being long and curved posteriorly. As in the other species the intestine (Fig. 10, *In.*) appears as a constricted groove on the right side of the cæcum, and does not become complete until it leaves the distal end of the sac, then it continues in a sinuous course (Fig. 8, *In.*) to the posterior part of the stomach, where it turns and passes as the rectum (Fig. 8, *R.*) over the posterior adductor muscle.

Concerning the branchia Dr. Ridewood says: "The plicæ of the outer demibranch have about 14, those of the inner about 18, filaments . . . The principal filament bears a false resemblance to a couple of ordinary filaments, due to the sharply-cut sides of the frontal groove, and to the fact that each of the halves is about the same size as an ordinary filament."

Psammobia tellinella, Lamarck.

External Characters. — The largest animal examined measures 25 mm. by 11 mm. The dorsal surface is very slightly triangular, but the remaining ones are curved, with the ventro-posterior part projecting more posteriorly, the same as in the other species.

The mantle-lobes are thin and possess the usual marginal muscular band, which, like that in *P. vespertina*, tapers towards the rear part of the animal. The mantle-borders have the three characteristic longitudinal folds, and the apposed surfaces of the middle and outer ones are nowhere fused except on the dorsal surface between the adductor muscles, but the inner ones coalesce over the whole of the dorsal surface of the posterior adductor and the greater portion of the anterior adductor. Between the anterior adductor and the musculus cruciformis is the large pedal aperture. Above the latter muscle the inner folds are first united, then they are connected with the external walls of the proximal portion of the siphon as in *P. vespertina*. The middle fold carries a tentacular fringe, and the pallium extends some distance posteriorly to the divergent inner fold, and is capable of quite enclosing the withdrawn siphonal tubes.

Comparatively the siphonal tubes (Fig. 11, *In.S.* and *Ex.S.*) do not appear to be so large or muscular as those of *P. vespertina*, and the proximal part of the siphon is not situated so far anteriorly. The foot is large and muscular, and usually lies in an anterior direction.

The anterior adductor muscle (Fig. 11, *A.A.*), situated on the antero-dorsal side, lies parallel to the edge of the mantle with its ends conforming to the convexity of the shell. There is only a slight indication on the ventro-posterior surface of the constricted part as noticed in *P. vespertina*. The posterior adductor muscle (Fig. 11, *P.A.*), somewhat ovate-shaped, is situated in the dorsal part at the posterior end of the animal, and its ends likewise conform to the convexity of the shell.

A lateral view of the retractor pedis anterior muscle shows it to be wide dorsally, and tapering ventrally, whilst the retractor pedis posterior muscle (Fig. 11, *P.R.P.*) is perhaps shorter and thicker